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Stand dynamics modulate water cycling and mortality risk in droughted tropical forest

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Abstract

Transpiration from the Amazon rainforest generates an essential water source at a global and local scale. However, changes in rainforest function with climate change can disrupt this process, causing significant reductions in precipitation across Amazonia, and potentially at a global scale. We report the only study of forest transpiration following a long-term (>10 year) experimental drought treatment in Amazonian forest. After 15 years of receiving half the normal rainfall, drought-related tree mortality caused total forest transpiration to decrease by 30%. However, the surviving droughted trees maintained or increased transpiration because of reduced competition for water and increased light availability, which is consistent with increased growth rates. Consequently, the amount of water supplied as rainfall reaching the soil and directly recycled as transpiration increased to 100%. This value was 25% greater than for adjacent nondroughted forest. If these drought conditions were accompanied by a modest increase in temperature (e.g., 1.5°C), water demand would exceed supply, making the forest more prone to increased tree mortality.

KEYWORDS

drought, sap flux, transpiration, tree mortality, tropical forest, water cycling

1 | INTRODUCTION

In South America, 25%–35% of precipitation is estimated to be recycled via repeated precipitation–evaporation processes as air masses travel west over Amazonian rainforest (Eltahir & Bras, 1994; Zemp et al., 2014). Up to 70% of the water resources of the extensive Rio de La Plata basin are dependent on evapotranspiration from Amazonia (van der Ent, Savenije, Schaeffli & Steele-Dunne, 2010). Changes in land cover properties in the Amazon basin can disrupt this recycling process, potentially causing significant reductions in precipitation both in Amazonia and regionally to the La Plata basin (Spracklen, Arnold & Taylor, 2012), with large economic consequences (Marengo, Alves & Torres, 2016). However, how tropical forest transpiration will respond to future drought and temperature change remains uncertain. Despite the climatological importance of large gross fluxes of transpiration from the world's tropical rainforests (Lawrence & Vandecar, 2015; Spracklen et al., 2012), predictions of how water recycling from tropical rainforest may change with climate, in particular climate extremes, are poorly constrained by data for this biome (Kume et al., 2011; Restrepo-Coupe et al., 2013). The frequency and intensity of subregional extremes in precipitation and temperature are predicted to increase this century, leading to increased drought at seasonal, interannual and decadal timescales (Duffy, Brando, Asner & Field, 2015; Fu et al., 2013). How water use by forests will change remains unclear. Tropical rainforests generally transpire 30%–70% of incoming rainfall (Kumagai, Kanamori, & Chappell, 2016), but at their climatic margins, where annual rainfall is 1,200–1,500 mm/year (Zelazowski, Malhi, Huntingford, Sitch & Fisher, 2011), this value rises to above 90% placing a cap on regional moisture supply, deep soil recharge and river run-off (van der Ent et al., 2010; Kume et al., 2011).

Processes ranging in scale from plant tissue to ecosystem can control how the proportion of rainfall that is recycled changes in response to drought. For individual trees, long-term responses may include physiological changes in water use efficiency, turgor regulation and the sensitivity of xylem hydraulics to cavitation, structural acclimation in new root growth (Eller, Lima & Oliveira, 2016; Oliveira, Dawson, Burgess & Nepstad, 2005), or changes in leaf to sapwood or root area ratios (Wolfe, Sperry & Kursar, 2016). These responses can help regulate gross water demand by the canopy, but ultimately it will be the demographic regulation of stand density via competition for water that will determine whole-system water use and stability (Meir, Wood et al., 2015).

Measurements of sapflux (J_s) are a powerful method to understand the annual and seasonal shifts in forest water use, including the relationship of transpiration to environmental variables (Eller, Burgess & Oliveira, 2015; Fisher et al., 2007; Poyatos, Aguade, Galiano, Mencuccini & Martinez-Vilalta, 2013) and the physiological plasticity associated with stomatal regulation in trees (Martinez-Vilalta, Poyatos, Aguade, Retana & Mencuccini, 2014). There are, however, relatively few reports of continuous sapflux (J_s)

measurements in tropical rainforest (Fisher et al., 2007; Granier, Biron, Breda, Pontallier & Saugier, 1996), none of which have been conducted following long-term drought (>5 years). Studies during long-term drought are essential to establish whether tropical trees can adjust their water use to drier soils over timescales approaching those of possible changes in climate. By imposing a reduction in soil water availability, large scale through-fall exclusion (TFE) provides a unique way to examine the processes underlying long-term responses to increased deficit in soil water potential, and to examine how water use and stand-scale water cycling are altered.

Here, we quantify the effects of a prolonged experimental soil drought on water use as a proportion of available rainfall by an old-growth tropical rainforest in eastern Amazonia. We use the world's only long-running tropical forest TFE experiment, at the Caxiuanã National Forest Reserve, Pará State, Brazil (da Costa et al., 2010; Meir, Mencuccini & Dewar, 2015; Rowland, Lobo-do-Vale et al., 2015), to compare how transpiration and through-fall recycling (the percentage of canopy through-fall transpired by the forest) are altered between a normal forest and a drought-treated forest, with the latter having experienced a 50% TFE treatment since 2002. We previously reported (Rowland, da Costa et al., 2015) the loss of about 40% biomass after 14 years since the TFE started. As measurements of stand scale transpiration were also available for the years 2002–2003, i.e., at the start of the experiment, but before the large waves of mortality occurred, we are also able to determine how total water use and its partitioning changed in response to changes in stand density and structure.

2 | MATERIALS AND METHODS

2.1 | Site

The site is a long-term TFE experiment located at the Caxiuanã National Forest Reserve in the eastern Amazon (1°43'S, 51°27'W). The site has a mean rainfall of 2,000–2,500 mm/year, a pronounced dry season between June and November (rainfall <100 mm/month) and is situated on *terra firme* forest, with yellow oxisol soils (Ruivo and Cuhha, 2003).

The TFE experiment consists of two 1 ha plots located on old-growth tropical forest. The treatment plot (TFE) has been covered with plastic panels and guttering 1–2 m in height since 2002. This structure excludes 50% of the incoming canopy through-fall. A control plot, on which no rainfall exclusion has taken place, is located <50 m from the TFE. For further details on the experimental design and results see: da Costa et al. (2010), Meir, Mencuccini et al. (2015), Meir, Wood et al. (2015), Rowland, da Costa et al. (2015) and Rowland, Lobo-do-Vale et al. (2015). Following 14 years of continuous drought the plot has experienced a 40% loss in biomass (equivalent to 100 Mg C/ha), this loss generated a substantial reduction in basal and thus sapwood area, a reduction in leaf area index (LAI) and an increase in light interception in the lower canopy (see Rowland, da Costa et al., 2015).

2.2 | Meteorological and soil moisture data

All meteorological variables were obtained from a weather station situated at the top of a 40 m tower located in the control forest. During the period of 2014–2016 air temperature, relative humidity, solar radiation and rainfall were monitored half hourly using HC2S3 (Campbell Scientific, Logan, UT, USA), CM3 sensors (Kipp and Zonen, Delft, The Netherlands), and a tipping bucket rain gauge (TE525MM; Campbell Scientific), respectively. Vapour pressure deficit (VPD) was calculated from temperature and relative humidity. Soil access pits are located in the control and TFE plots. In each soil access pit volumetric soil water content sensors (CS616; Campbell Scientific) have been placed at depths of 0, 0.5, 1, 2.5 and 4 m, to monitor soil moisture every hour (cf. Fisher et al., 2007; for full methodology). Here, we use the data collected during 2014–2016, the period during which sapflux (J_s) data were collected. Hourly relative extractable water (REW) aggregated across the first two metres was calculated using the soil moisture data and following the methodology in Meir, Mencuccini et al. (2015) and Meir, Wood et al. (2015). Daily values were calculated using a 30 day running mean so that the seasonal trend of REW was captured, rather than daily or hourly spikes in soil water concentrations.

2.3 | J_s data

J_s was measured using the heat balance method (Cermak, Deml & Penka, 1973; Cermak, Kucera & Nadezhdina, 2004; Kucera, Cermak & Penka, 1977) and previously used at the site (Fisher et al., 2007). EMS51 sensors (Environmental monitoring systems; <http://www.emsbrno.cz>), were used on all trees. The installation process and functioning of these sensors are described in the Supporting information. Between November 2014 and December 2016 the EMS51 sensors were installed on 16 trees in the control plot and 13 trees in the TFE plot. The start date of sampling varied among trees (see Table S1). Trees for which sensors were installed in 2016 (seven on the control and three on the TFE) were excluded from the upscaling analysis (see below) on the basis that they had an insufficient data time series. To ensure we could upscale with confidence, sensors were strategically placed across trees with a range of diameters at breast height (DBH) values (15–56 cm) and on common species in the control and TFE plots known to be both sensitive and resistant to drought stress (see Table S1).

Values of J_s obtained from the EMS51 sensors were always offset from zero as a constant part of the heat loss from the heated electrodes is conducted into the xylem tissue. To remove this effect the data were baselined, as performed in other standard sap flux processing protocols (e.g., Poyatos et al., 2013). To baseline the data, the minimum value of the J_s for each night was subtracted from all values for the subsequent day, provided evaporative demand was low (preventing night-time J_s , VPD < 0.15 kPa). If night-time VPD > 0.15 kPa, a minimum value was linearly interpolated from the baseline values from surrounding days using the *approx* function in R (R Core team 2014).

2.4 | Gapfilling J_s data

Gaps in the data varied from 0% to 63% (average of 8%) and were generally caused by power failure or broken sensors. Gaps in the hourly baselined J_s data since sensor installation were gap-filled using an autoregressive (AR1) style model, accounting for the autocorrelation in the data. Firstly, the *boxcox* function in R was used to determine the lambda value to power transform the J_s data of each tree (lambda range 0.46–0.84). Secondly, a linear regression was performed between the power-transformed J_s , the three independent variables VPD, radiation, REW and six vectors of the power-transformed J_s preceding the dependent variable by 1–6 hr. We correlated each J_s data point with the six hourly data points preceding it, as this was the number required to remove the autocorrelation effect across all trees (determined using ACF plots). Data from all but one of the trees were gap filled with a model which had an $r^2 > .90$; the mean model fit was $r^2 = .93 \pm 0.07$ (SEM), demonstrating a very good fit between modelled and measured J_s .

2.5 | Statistical analysis

All statistical analyses of J_s data were conducted within R 3.0.2 (R Core Team³⁵) and all errors are shown as standard deviation. To compare diurnal responses between plots and seasons an average diurnal J_s pattern was calculated for the control and TFE plots, during peak wet and dry season. Peak wet and dry season were determined as the 2 months with the highest (October and November) and lowest (March and April) monthly average VPD. Multiple linear regressions between mean daytime transpiration rate per tree, per plot (calculated as the average J_s from all trees per plot) and environmental conditions were fitted to estimate the most important environmental controls on daily J_s . Initially VPD or temperature with radiation, and REW were included in the model and sequentially nonsignificant variables were excluded in stepwise linear regressions determined by Akaike's information criterion. For the TFE the use of a single model across both wet and dry season was compared to the model fit of using separate wet and dry season models (considering wet season as Feb-Jul and dry season as Aug-Jan). Two models were most effective on the TFE (see Results) and the same seasonal modelling approach was followed with the control plot. The *relaimpo* package in R (Grömping, 2006) was used to calculate the proportion of the explained variance which was accounted for by each variable retained in each of the final models.

Seasonal relationships of VPD to J_s were created by fitting a sigmoidal function using the *SSlogis* function in R through average hourly J_s data for the trees on the control and TFE, binned by VPD classes. Separate relationships were created for peak wet and dry season and the data were normalized using the maximum average J_s , across plots and seasons, to make the relationships comparable between plots and seasons.

2.6 | Scaling J_s to calculate plot-scale transpiration and its temperature sensitivity

Scaling J_s from the measured trees for the measured periods to plot level at the yearly time scale involved the following steps to properly propagate the sources of uncertainty deriving from tree-to-tree variability in J_s as well as uncertainties in the scaling of J_s with tree DBH.

To obtain a scaling relationship between tree J_s and DBH, we regressed J_s data from April to May 2015 (i.e., peak of wet season and when tree DBH were measured) against DBH. This allowed us to additionally include data obtained by Fisher et al. (2007); also collected at peak wet season); all data were obtained using the same measurement method (Environmental monitoring systems; <http://www.emsbrno.cz>). There was a linear relationship between DBH and mean daytime J_s , with an r^2 of .39 and $p < .01$ (Fig. S1). This scaling relationship was assumed on the control and TFE plot based on similarity of J_s values across the two plots during the wet season (see Results section), and it was applied to the DBH of all trees on both plots measured in 2015 (see Rowland, da Costa et al., 2015, for further details). To account for the uncertainty in the parameters of this relationship, 1,000 parameter estimates were randomly generated from the model using the covariance matrix for the intercept and slope. These parameters were used to create 1,000 estimates of average daytime April and May J_s for all trees >10 cm DBH on both plots. The average daytime J_s values for each tree, for each of the 1,000 parameter combinations, were then summed to give 1,000 plot-scale estimates of transpiration for April and May of the measurement years, accounting for the error on our DBH to J_s relationship. Following this, a second procedure was employed using similar principles to propagate uncertainty from 1,000 estimates of the measured April–May data to the whole year and across the two plots. We employed the best-fit multilinear model per plot, which described how mean daily J_s varies with climate variables (see above). Because of the strong autocorrelation between VPD, RH and air temperature, only the best regressor among these three was finally employed in the upscaling procedure (see Supporting information for further details). Besides the two estimates for the Control and TFE plots, a third estimate of plot-scale transpiration was generated by applying the estimated J_s from the multiple regression models of Control to the standing biomass of TFE. This estimate gives downscaled values of transpiration on Control with the effect of the loss in basal area on the TFE imposed on Control, and the changes in transpiration rates with environmental variables remaining equal to those on Control.

To estimate the effects of increasing temperatures on plot scale transpiration, the 1,000 model coefficients from above were rerun with temperature, relative humidity and VPD altered according to a 1.5, 2, 3, 4 and 5°C increases in mean air temperature. We emphasize that the purpose of these temperature rise scenarios is not for future prediction, but to estimate the effects of long-term drought on the sensitivity of the forest to other changes in climate. The scaling procedure was then repeated as above. The transpiration rates

at each temperature level were then compared to the canopy through-fall received by each plot assuming a canopy storage term of 21.5% on the control plot, as measured at the site in 2008 (Oliveira, Da Costa, Da Costa, Sousa & Braga, 2008; and within the ranges of canopy storage terms measured across other Amazonian forests (Czikowsky & Fitzjarrald, 2009)). On the TFE we scaled down this estimate of canopy storage to 18.1% (Oliveira et al., 2008), in proportion with the leaf area index measured in TFE relative to Control (See Rowland, da Costa et al., 2015), assuming that canopy interception decreases proportionally with leaf area. The analysis was also repeated using a canopy storage term of 12% (Czikowsky & Fitzjarrald, 2009) to account for uncertainty in throughfall resulting from differences in LAI across plots (see sensitivity to canopy interception term section). Also we would expect it to provide a lower limit to the sensitivity in TFE because of fewer interception surfaces in TFE (i.e., lower LAI and biomass; Rowland, da Costa et al., 2015). However, due to an inability to accurately estimate LAI on a per tree basis, which may have changed over time due to the treatment effect and due to the likely increase in atmospheric coupling on the drought relative to the control plot due to increasing mortality over time, we were not able to accurately scale sapflux according to leaf area to estimate differences in leaf level conductance between the plots (e.g., Eller et al., 2015).

3 | RESULTS

During the study period (November 2014–December 2016) there were strong seasonal changes in relative extractable water (REW), precipitation and moderate seasonal changes in vapour pressure deficit (VPD) at our study site (Figure 1). An El Niño event took place across Amazonia in 2015–2016, but had limited distinctive influence on climate drivers at our site, which is demonstrated by the El Niño year not creating substantial climate anomalies relative to previous years (Fig. S2). Therefore, considering 2015 to represent standard climatological conditions, we find average transpiration is $1,389 \pm 279$ (SD) mm/year on the control forest plot. On the TFE forest plot a transpiration rate of 964 ± 245 (SD) mm/year in response to the 50% experimental reduction in throughfall was observed; this represents a 30% decline in transpiration relative to the control. Transpiration therefore comprised 75% (SD range = 60%–90%) of canopy through-fall on the control, compared to 101% (SD range = 75%–127%) on the TFE (Figure 2). These estimates of through-fall recycling at Caxiuanã are similar to the mean values previously quantified at the start of the TFE treatment for the years 2002–2003 using updated estimates for canopy interception for the plots (59%–71% and 78%–103%, control and TFE, respectively, Figure 2). These estimates are robust to assumptions made regarding the magnitude of canopy rainfall interception as a proportion of total rainfall and to differences in canopy storage caused by different values of leaf area index across plots (see Table S2).

Relative to the control, we observed changes in the transpiration rates of trees on the TFE (Figure 3). However, there was only a 5% difference between 2015 transpiration on the TFE and the

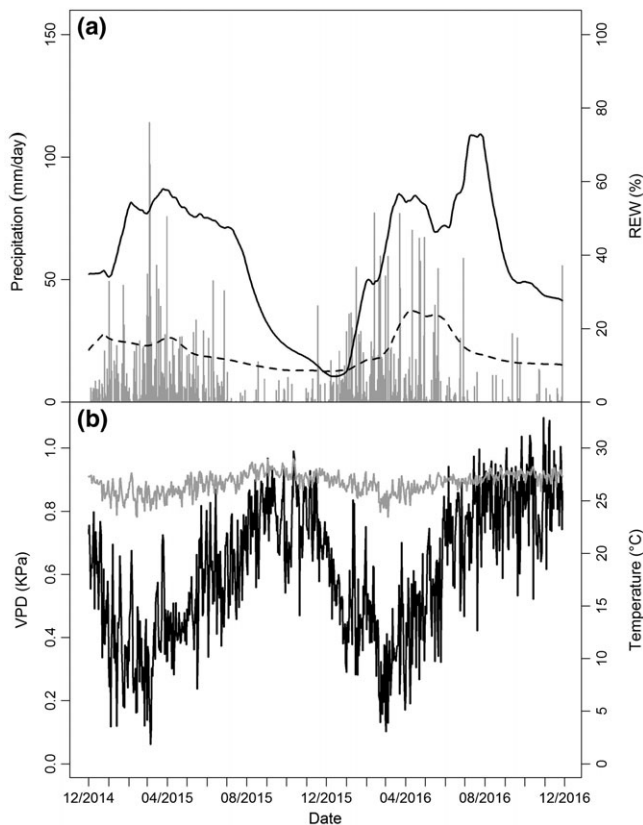


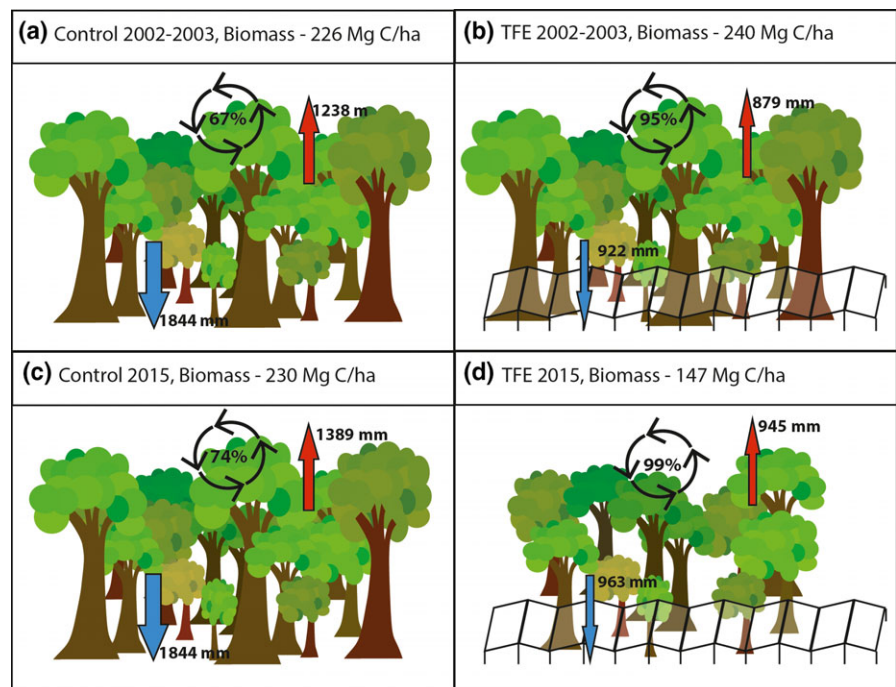
FIGURE 1 Meteorological data for the Caxiuanã site during the sapflux measurement period. In panel (a), precipitation (mm/day) is shown as grey bars alongside average daily relative extractable water (REW) integrated across three metres soil depth for the control plot continuous black line) and TFE plot (dashed grey line). Panel (b) shows average daily air temperature (°C, grey line) and average daily VPD (kPa, black line)

transpiration expected if estimates from the control were down-scaled to reflect the 40% reduction in biomass and related basal area which occurred between 2002 and 2015 (Figure 2). This small reduction by low dry season transpiration was countered with higher wet season transpiration on the TFE (Figure 3). Increased seasonality in TFE transpiration meant that daytime J_s was modelled more effectively using a separate multiple regression model for dry (Aug-Jan) and wet (Feb-Jul) season on the TFE (r^2 dry = .60, r^2 wet = .69, r^2 whole year = .61, all p values < .01). Dry season variation in transpiration on TFE was explained mostly by REW (44%) and radiation (47%). During the wet season, radiation explained 60% of the variance, VPD 33% and REW 7%. On the control plot air temperature (32%) and radiation (67%) controlled dry season transpiration (r^2 = .81) and radiation (65%) and VPD (35%) were the most important for controlling wet season fluxes (r^2 = .72).

The reduced dry season transpiration flux on the TFE (Figure 3) was caused by substantially lower peak daytime (11 a.m.–4 p.m.) fluxes in the dry season (Figure 4b) compared to the wet season. In contrast, the control plot maintained higher J_s throughout the day in the dry season relative to the wet (Figure 4a), suggesting low REW constrained J_s during periods of high atmospheric demand on the TFE. The REW constraint resulted in an altered relationship between J_s and VPD in the dry season on the TFE, contrasting with the wet season relationship, which was similar to that observed on the control (Figure 5). However, this increased seasonality had a limited effect on plot-scale reductions in transpiration relative to the effect of the loss of biomass and related basal area and active sapwood area (Figures 2 and 3).

Using the multivariate linear models which specified how J_s varied with environmental conditions on the control and TFE plots (see

FIGURE 2 How transpiration per year (red arrows), canopy through-fall per year (blue arrows) and annual through-fall recycling rate (% circular black arrows) change on the control (a, c) and TFE (indicated by panel structure b, d) plots from 2002 to 2003 (a, b) to 2015 (c, d). The diagram depicts the change in above ground biomass and the shift in forest structure which occurred during the full experimental period because of tree mortality on the TFE



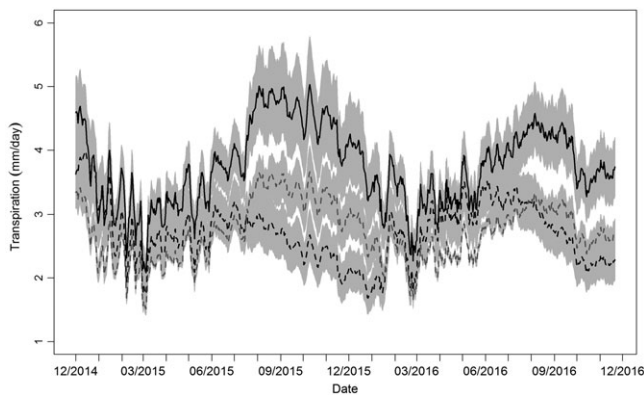


FIGURE 3 Daily transpiration (mm/day) from December 2014 – July 2016 for the control plot (black line), the TFE (dashed black line), and the estimated transpiration flux from the control plot if its values were downscaled to reflect only the effect of basal area loss on the TFE plot (dashed grey line). Grey shaded area shows the SE on the estimates calculated using a bootstrapping technique (see Methods)

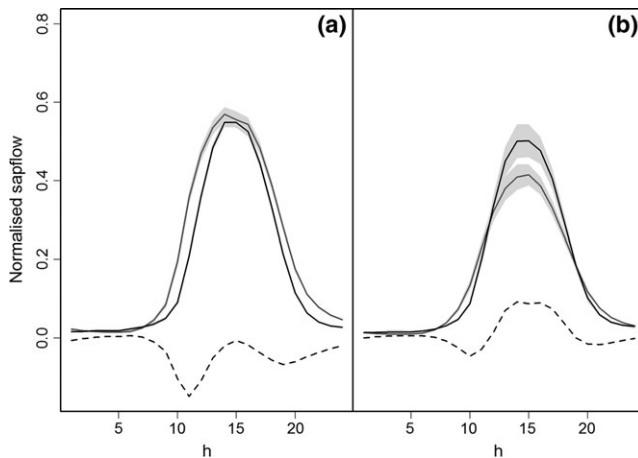


FIGURE 4 Average diurnal J_s patterns normalized using seasonal maxima per tree during peak wet (March and April, solid black line) and peak dry season (October and November, solid grey line) for trees on control (a), and TFE (b). The black dashed line shows the peak wet minus the peak dry season response for each panel and the grey shaded area shows the SE

Methods), we explored how transpiration would vary on both plots if an increase in mean temperature of 1.5–5°C and the resultant increases in VPD were imposed, assuming all else remained equal. The increase in absolute transpiration with a 5°C increase in temperature was greater on the control than the TFE, but was proportionally similar (20%, Figure 6a). However, the TFE would risk exceeding the imposed canopy through-fall supply even at the lowest temperature rise tested (1.5°C, Figure 6a). In contrast, even with a 5°C rise in temperature, the control forest only reaches a through-fall recycling rate of 91% for transpiration, still below that of the TFE within the current climate. In addition, both control and TFE recycle >100% of the water they receive between July–December (dry season) under current climate (Figure 6b), with this value increasing

substantially with a 5°C rise in temperature (Figure 6c). Under the current climate, between July and October the TFE forest transpires more than six times the precipitation it receives and this rises to almost eight times with a 5°C rise in temperature, creating a substantially greater imbalance between transpiration and precipitation (Figure 6b,c).

4 | DISCUSSION

Until now the long-term responses of water use in a tropical forest exposed to soil drought stress have not been studied. With new sapflow data spanning a 2-year period we are able to demonstrate that the 40% loss of forest biomass observed on the TFE (Rowland, da Costa et al., 2015) resulted in a 30% reduction in total forest transpiration. We are also able to demonstrate for the first time that the surviving trees are able to maintain or increase their transpiration rate on a per-tree basis, causing 100% of the available rainfall received by the droughted forest to be used for transpiration. Furthermore, we demonstrate that if such drought conditions were combined with a mild temperature rise, further tree mortality would be inevitable, as forest water demand would substantially exceed supply over an annual and multiannual timescale.

Our estimates of transpiration rates and through-fall recycling rates (Figure 2, Table S2) are consistent with previous measurements and modelling at this old-growth rainforest site (Carswell et al., 2002; Fisher et al., 2007). They suggest a remarkably constant water flux partitioning over the 15 years of the experiment, despite a substantial shift in forest structure because of high mortality in the TFE-treated plot. The increase in the recycling rate to 100% on the TFE suggests that a high sensitivity by the trees to atmospheric demand for water is maintained even following long-term drought. Our data suggest that drought-induced mortality of the tallest trees changed stand water use patterns, facilitating greater growth competition in the lower canopy, thereby maintaining very high levels of through-fall recycling on the TFE. This is consistent with the observation (Rowland, da Costa et al., 2015) that small- and medium-sized trees increased their growth rates after mortality of the taller trees, by responding plastically to increased light availability in the lower canopy. This hypothesis is also consistent with current hydraulic theory, which suggests that trees will continue to compete for, and use up, a limited water supply, provided the advantages accrued from the related carbon gain exceeds the cost of hydraulic damage (Sperry & Love, 2015; Wolf, Anderegg, & Pacala, 2016). Plastic reductions in water use as REW declines from wet to dry season on the TFE are likely to only partially alleviate the water stress (Figures 3 and 4), which would be substantial during climate extremes, and would impose increased tree mortality risk. The intense regrowth by small-to-medium diameter trees (Rowland, da Costa et al., 2015) is therefore likely to be the primary driver maintaining through-fall recycling at the high levels seen in 2002–2003.

Following the mortality of the largest trees, competitive release of small-to-medium diameter trees considerably elevated wet season

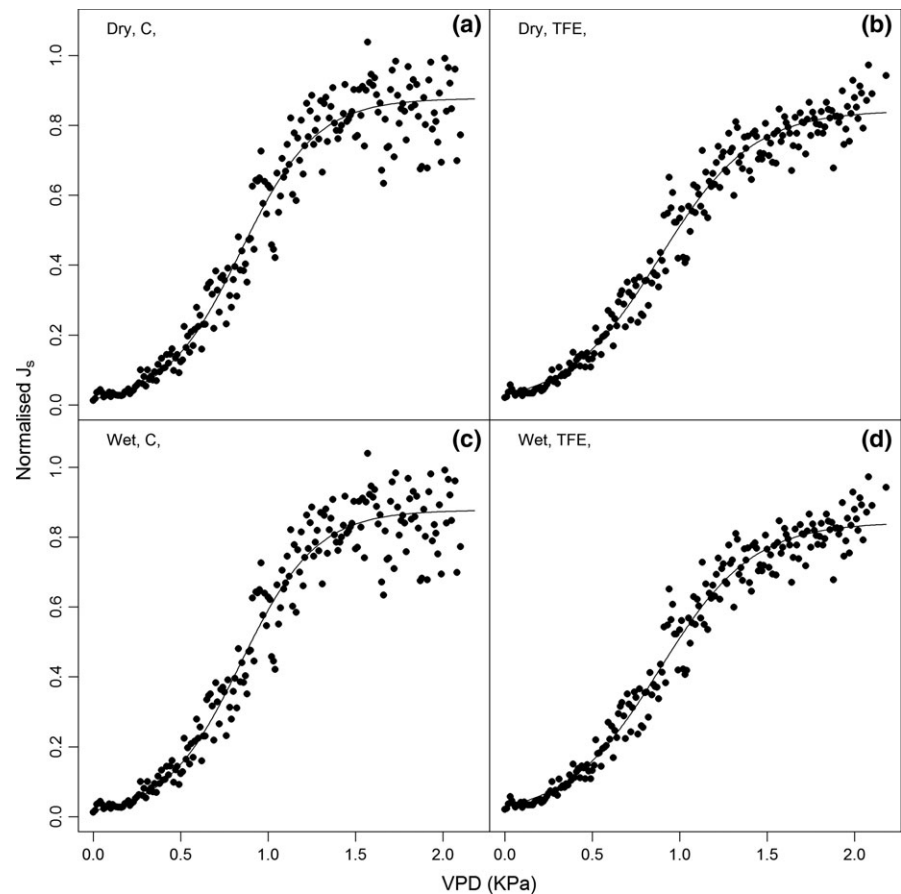


FIGURE 5 Optimized sigmoidal relationships between J_s and VPD for trees on the control (C, a & c) and TFE (b & d) plot in peak dry and peak wet season. J_s is binned by VPD and normalized by max hourly J_s per year to make relationships comparable across plots and season

stem growth on the TFE (Rowland, da Costa et al., 2015). As transpiration accompanies photosynthesis and responds to increased radiation availability, it is possible that the TFE trees have acclimated, with elevated water use in the wet season to maximize growth, and restricted growth in the dry season (Figures 2 and 3), thus explaining the increased seasonality in transpiration observed on the TFE (Figure 1). Our sample size prevents us from examining whether sap flux from small-to-medium diameter trees increased relative to large trees. Comparison of sap flux values and canopy through-fall in 2002/03 with those in 2015 provides indirect confirmation of similar levels of competition for water following mortality-related release on TFE. Yearly stand-scale sap flow values on the TFE were estimated as 953 and 805 mm in 2002/03 vs. 945 mm in 2015 (Table S2). Therefore, despite a 40% biomass reduction, water use remained similar over time on a per unit ground area, but increased on a tree-level basis on the TFE, due to having fewer trees per unit ground area. However, we note that our LAI measurements estimate only about a 12%–20% reduction in leaf area on the TFE relative to Control (see Rowland, da Costa et al., 2015), significantly lower than our estimate of a 30% reduction in transpiration. Measurements of LAI in complex multilayered canopies are notoriously challenging (Breda, 2003) and these difficulties may explain the discrepancy between the two estimates.

A shift from radiation and air temperature controlling dry season transpiration on the control plot, to REW and radiation controlling it on the TFE suggests that trees on the TFE adjusted to limit water

use during the dry season when REW was low. The strong controlling influence of REW on dry season transpiration on the TFE, but not the control plot suggests low REW restricts dry season transpiration and is most likely linked to significant hydraulic stress as water demand approaches or exceeds supply on seasonal time-scales (Figure 6). Relative to Control, the TFE forest maintains higher through-fall recycling rates also in the wet season (January to June) when precipitation levels are substantially elevated (Figure 6b,c), resulting in a reduced capacity to recover from dry season water stress. Given predicted changes in VPD, and thus leaf water potential, combined with lower soil water potentials, under some future climate scenarios, there is potential that trees could rapidly be pushed beyond their species-specific hydraulic safety margins (the difference between normally occurring minimum xylem pressures, and those causing damage to xylem tissues and restricting water transport), potentially causing xylem embolism (Sperry & Love, 2015; Sperry et al., 2016) and/or leaf loss, with the ultimate risk of increased drought-induced mortality. Furthermore, as total annual tropical forest water use approaches total soil water supply, the likelihood of hydraulic damage occurring in the xylem becomes greater. This is particularly the case for large canopy-top trees, which are exposed to greater variability and extremes in VPD, high air temperatures, and larger xylem tensions (Bennett, McDowell, Allen & Anderson-Teixeira, 2015; McDowell & Allen, 2015), which together have been hypothesized to lead to a series of processes causing drought-induced mortality (Anderegg et al., 2016; McDowell & Allen, 2015;

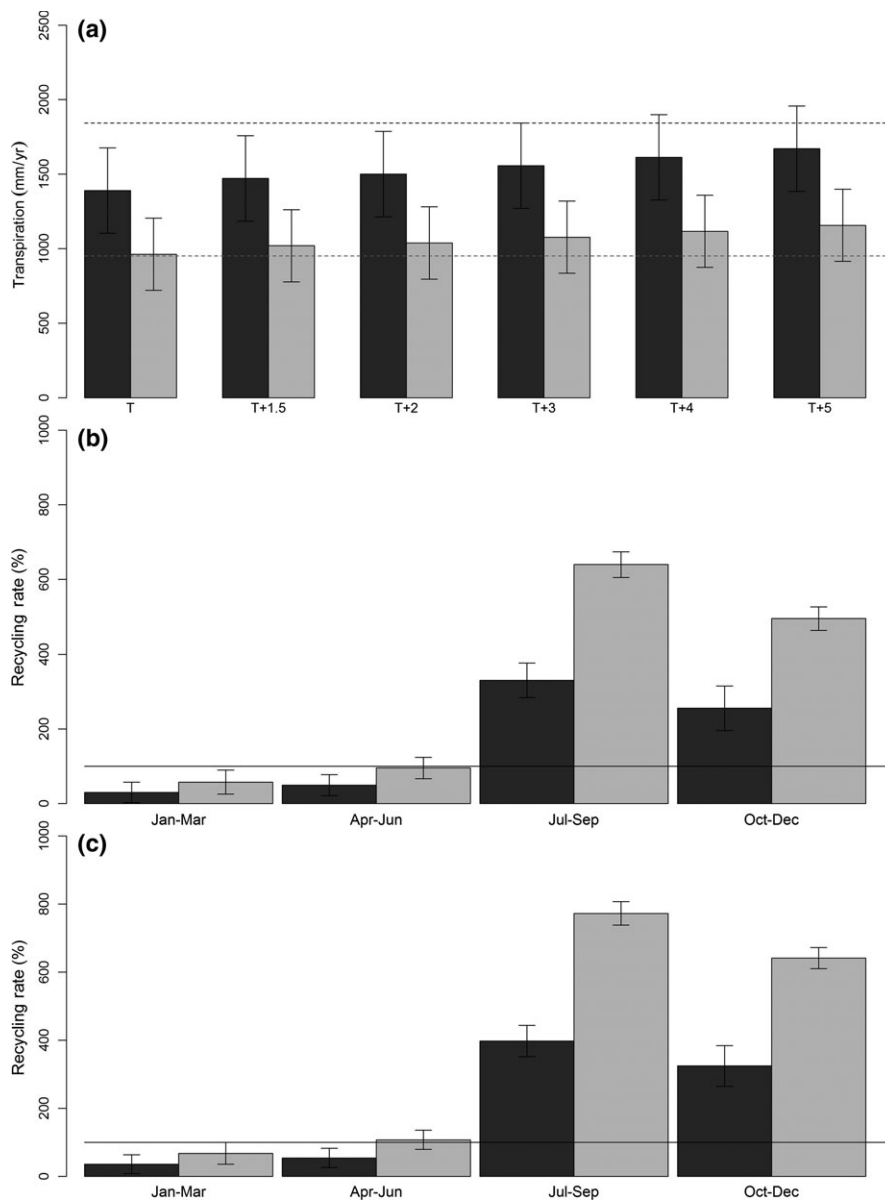


FIGURE 6 The effect of increasing temperature on annual transpiration fluxes for control (C) and TFE (a), under current temperature climate (T, year 2015 used) and under the climate of this year + 1.5, 2, 3, 4, and 5°C, accounting for temperature-driven changes in relative humidity and vapour pressure deficit. Dashed lines (a) indicate the rainfall reaching the forest floor on control (black) and TFE (grey). Rainfall reaching the forest floor is estimated from rainfall minus a canopy interception estimate of 21.5% (see Methods). Panel (b) and (c) show the % of seasonal through-fall recycled as transpiration during the four quarters of the year, under the current climate (b) and with a 5°C increase in temperature (c). Solid lines in (b) and (c) indicate 100%, where transpiration exceeds the rainfall reaching the soil. Error bars show the SD across the 100 estimates made of each scenario (see Methods)

Mencuccini, Miniunno, Salmon, Martinez-Vilalta, & Hölttä, 2015; Rowland, da Costa et al., 2015; Sperry et al., 2016; Wolfe et al., 2016).

In future climate scenarios, areas of tropical forest experiencing drought stress are also likely to experience increases in temperature well beyond the moderate levels of 1.5–2°C (Christensen et al., 2007; Duffy et al., 2015; Fu et al., 2013; Sanderson, O'Neill & Tebaldi, 2016). Using a novel modelling approach, we demonstrate here that a forest exposed to long-term drought is far more likely to have transpiration demand exceed supply than a nondroughted forest (Figure 6). This is driven mostly by transpiration rates exceeding precipitation supply in the dry season by up to eight times in a droughted forest simultaneously experiencing temperature-driven rises in VPD, as would be expected during natural drought. This puts a very large strain on soil water supply, which the nondroughted forest can easily buffer, due to the higher overall wet season recharge of soil water from higher precipitation. Without this recharge we demonstrate that even

a very moderate rise in temperature necessitates tree mortality to balance transpiration demand and soil water supply. Although a 50% decline in canopy through-fall on a 10 year time-scale is unlikely within current climate projections, reductions of up to 50% are predicted across parts Amazonia, in a range of recent climate scenario analyses (Christensen et al., 2007; Duffy et al., 2015). This result thus has strong implications for future climate change and carbon cycle feedback predictions, as it suggests that tropical trees will maintain substantial transpiration fluxes even in the face of drought and rising VPD, and that the forest appears to maintain a similar water balance through the process of tree mortality.

The overall picture emerging from these results is that compensation processes acting at tissue, tree and stand level have maintained the high levels of through-fall recycling on the TFE-treated forest over more than a decade. While high mortality tended to reduce levels of competition for water, the mortality-related growth release for small-to-medium sized trees tended to increase it.

Additional processes, such as acclimation in leaf:sapwood and leaf:root ratios could also have affected competition for water. Estimated through-fall recycling rates are already at approximately 100% on the TFE after 15 years of reduced soil moisture availability, suggesting that further demands for water can only be facilitated by additional tree mortality. As recycling rates are already >100% in the dry season, even in undroughted forest, it suggests that rainforest trees must rely on soil (and likely internal) water storage to carry them through to the next wet season, potentially limiting their capacity to maintain carbon uptake, whilst simultaneously also elevating their mortality risk. If the effects of our 50% rainfall reduction, or indeed a similar reduction in basal area imposed by widespread logging, were to occur at a large scale, even the minimum increase in atmospheric temperature which is now deemed unavoidable in the coming century would imply severely reduced deep soil water recharge and run-off, and increased tree mortality risk. The potential implications for regional economies, water supply and climate-carbon cycle feedbacks are substantial.

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